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Abstract
The authors presented people (Experiment 1) and pigeons (Experiments 2 and 3) with a large number of 1-way traveling salesperson problems that consisted of 3, 4, and 5 identical stimuli (nodes) on a computer monitor. The sequence of nodes that each traveler selected was recorded, and the distance of the route was subsequently determined. The routes the pigeons and people selected were reliably more efficient than those used by a Monte Carlo model given the same problems. The pigeons' routes were significantly less efficient than a nearest neighbor model of performance, however. In Experiment 3, pigeons were required to select a route that was within the top 33% of all possible solutions for a given problem. The pigeons' solutions were significantly more efficient than those observed in Experiment 2, in which the behavioral criterion was not imposed. The mechanisms that pigeons and people may have been using to solve the traveling salesperson problems are discussed.

Keywords: traveling salesperson problem, navigation, route learning, problem solving

Imagine that you are a traveling salesperson. You depart your home on a multiday trip in which you will visit a number of communities where you will try to sell your products. One problem you encounter is to determine a route that will allow you to travel efficiently to all of the communities in which you need to sell your wares before returning home. An inefficient route will lead to increased time spent in a car, bus, train, or plane, as well as to decreased time spent interacting with customers.

The *traveling salesperson problem* (TSP) is the task of determining an optimal route through several points before returning to the starting point. The TSP has been extensively studied by mathematicians examining optimization problems (see Junger, Reinelt, & Rinaldi, 1997; Lawler, Lenstra, Rinnooy Kan, & Shmoys, 1986). To a lesser extent, TSPs, or analogues of the problem, have been used to study spatial cognition by researchers in the cognitive and behavioral sciences (Gallistel & Cramer, 1996; MacDonald, 1994; MacDonald & Wilkie, 1990; MacGregor, Ormerod, & Chronicle, 1999, 2000; MacGregor & Ormerod, 1996; Vickers, Lee, & Dry, 2006). The number of possible solutions or routes to a TSP increases as the number of locations or *nodes* in the TSP increases. With 5 locations, there are 12 possible routes (if the direction of travel is ignored); with 10 locations, there are 181,440 possible travel routes! Although the TSP has been investigated primarily as a conceptual problem, it also would appear to characterize the everyday spatial behavior of humans and numerous nonhuman animals.

Many nonhuman animals depart a place of shelter to visit one or more patches in their environment that contain resources before returning home. Nonhuman animals may be particularly adept at selecting an efficient route when given several foraging sites to visit because the cost of an inefficient route through these sites may include increased predation, lower rates of resource intake, increased energy spent traveling, as well as loss of time spent engaging in nonforaging activities, such as reproduction. Indeed, evidence from behavioral ecology indicates that animals are sensitive to the economics associated with their foraging. For example, starlings make hundreds of trips each day from their nest to different foraging sites where they pick up invertebrates to feed their young. The number of prey that the starlings retrieve during a given foraging excursion depends in part on how far away the foraging site is from the nest. The starlings take fewer invertebrates if the time to make the round trip to the foraging site is relatively short, whereas they take more invertebrates if the time to make the round trip to the foraging site is relatively long (Kacelnik, 1984; Kacelnik & Cuthill, 1987). Likewise, given a choice to visit one of two sites, many primates will visit a nearby foraging site first before traveling to a more remote site, unless the distant site contains a substantially more desirable resource (Janson, 1998). These data suggest that animals are well prepared to evaluate the economics of selecting among different routes, as encountered in the TSP.

How does a traveler select one route among a large number of available alternatives? Investigations using TSPs are important because they may provide insight into the spatial cognitive abilities of the travelers solving them. Menzel (1973) was

one of the first researchers to use an analogue of the TSP to investigate the spatial behavior and memory of chimpanzees. A young chimpanzee was carried around a large compound by one researcher. A second researcher walked with the pair and hid food in each of 18 locations inside the compound as the chimpanzee watched. After the locations had been baited with food, the focal animal as well as five other chimpanzees that had not been with the experimenter were released and allowed to recover the hidden food. The informed animals tended to search at locations where the researcher had placed the food. In addition, the routes that the informed chimpanzees took were different from those used by the experimenter; these routes appeared to be relatively efficient in terms of minimizing the distance the chimpanzees had to travel.

The route-minimizing behavior of the informed chimpanzees in Menzel's (1973) study is consistent with the notion that the chimps were using a *cognitive map* (Gallistel, 1990; O'Keefe & Nadel, 1978; Shettleworth, 1998; Tolman, 1948) of the goal locations to determine an efficient route during food recovery. A relatively conservative definition of a cognitive map would be a representation of the metric relationships among important locations than can be used to determine efficient routes (including novel routes). Although cognitive maps remain controversial (Bennett, 1996), it would appear that the chimpanzees' behavior was consistent with a stored representation of the spatial relationships among several goal locations.

The idea that the chimpanzees in Menzel's (1973) study were able to select an efficient route among several alternatives, perhaps by using a cognitive map, was further bolstered by a study conducted by Gallistel and Cramer (1996). Gallistel and Cramer had vervet monkeys retrieve food hidden at four goal locations that were positioned at the corners of a diamond. In one condition, the monkeys were required to make a round trip from the starting point to each of the three other goal locations before returning home. In a second condition, the monkeys were required to make only a one-way trip from the starting location to the other three locations. The most efficient route for the round trip was one that followed the perimeter of the diamond, whereas the most efficient route for the one-way trip required the monkey to cross the diamond along the midsection. Notably, when the monkeys were required to make a round trip, they tended to use the perimeter route, but when they were required to make a one-way trip, they tended to use the crossing route. This pattern of results indicates that the monkeys planned a particular route in advance of traveling on the basis of the configuration of the goal positions and the task requirements, again suggesting the use of a representation of the array of destinations.

Although the work discussed above has been promising, investigations using TSPs with nonhuman animals that have precisely measured the efficiency of the animals' routes or compared the efficiency of different routes to chance performance or other heuristic models have been limited. Such investigations are important, as they may provide fresh insights into the spatial cognitive abilities and spatial representations of the traveler. In addition, almost all of the studies using the TSP as a paradigm have been conducted with primates (however, see Bures, Buresova, & Nerad, 1992); TSP studies with other species would be of considerable interest. In Experiment 1 of the current study, we examined how human participants solve TSPs on a computer monitor as a bridge to past work with people. In Experiments 2 and 3, we used nearly identical procedures to examine how pigeons solve TSPs presented on a computer monitor in an operant chamber.

Experiment 1

In Experiment 1, we investigated people's ability to solve simple analogues of TSPs with three-, four-, and five-node routes presented on a computer monitor. In contrast to a true TSP, the participants were not required to return to the starting point; thus, they were required to make only a one-way trip (for convenience, we refer to the problems as TSPs instead of analogues of TSPs for the balance of this article). Although humans previously have been studied for their ability to solve TSPs (MacGregor & Ormerod, 1996; MacGregor et al., 1999, 2000), to our knowledge, such tests have been limited to participants using a pen to connect dots (nodes) on a piece of paper. This approach is useful, but the number of problems that can be administered to participants and the efficiency with which the data can be analyzed are limited. Hence, it would be useful to see whether human participants can solve an analogue of the TSP on a vertically mounted video display and whether their performance would be comparable to that reported in other studies when the problems have been administered using pen and paper. Finally, Experiment 1 allowed us to compare the performance of humans with pigeons (Experiments 2 and 3) when both were given comparable problems.

Method

Participants and apparatus. Eighteen adult female undergraduate students who had normal or corrected to normal vision and ranged in age from 18 to 23 years were studied for their ability to solve TSPs. The participants gave informed consent prior to participating in the study and received course credit.

Human participants were seated in a chair in front of a 15-in. high-resolution LCD monitor (NEC/Mitsubishi Model 1530V) positioned on a counter in a quiet laboratory. The height of the chair was adjusted so that the stimuli presented during an experimental session were viewed from a distance of approximately 0.5 m (3.67° × 3.67° of visual angle).

Procedure. When the participants entered the laboratory, they were asked to read and sign an informed consent form. If the participant elected to continue, she then was seated in a chair facing the computer monitor and testing began. During the course of trial, a start stimulus (a black cross on a white background) appeared in the center of the screen to signal the onset of a trial. The participant was required to position a cursor over the start stimulus and click the computer mouse to advance the trial. The start stimulus disappeared from the screen and, immediately thereafter, a display of three or more identical nodes (squares) appeared on the computer monitor. Each node was a white square (side = 2 cm) that had slightly rounded corners. A single black-and-white icon (i.e., an image of a compass) was visible in the center of the node. The position of each node was randomly determined with the constraint that the minimum distance between the nodes was 6 cm center to center. Thus, every problem had a unique spatial configuration, and every participant received different problems during a trial. The participant positioned the cursor over the node and clicked the mouse to select a node; the node was then highlighted to indicate that it had been selected. A

participant could select any of the three nodes as the starting node; the participant then was required to select the two remaining nodes just once without returning to a node that had been previously selected. If the participant returned to a previously selected node, a tone sounded, and the screen went black for 20 s prior to the start of a correction trial. The trial then was repeated with the same configuration of three nodes until the participant correctly selected all of the nodes at least once without revisiting a node. When the participant finished selecting all of the nodes in a problem, a double tone sounded, indicating that she had successfully completed the trial and that the next trial would begin shortly.

Prior to the start of the study, the experimenter told participants to select a node and try to find the shortest route to pass through each of the remaining nodes on the screen. The participants were also allowed to complete a warm-up trial with the experimenter to ensure that they were familiar with the experimental procedures. The experimenter did not provide feedback about the efficiency of the route during the warm-up trial. The participants were presented with 96 one-way analogues of the TSP that included, in sequence, 32 problems with three nodes, 32 problems with four nodes, and 32 problems with five nodes during the single experimental session. The participants had an unlimited amount of time to complete each problem.

Measures and analyses. We recorded the sequence of nodes that the participants selected for each problem, which we refer to as the *route* or *solution*. Using this information, in conjunction with the Cartesian position of each node, we were able to construct the total distance (in centimeters) of each route as a measure of performance. Note that in all of the analyses described below we use distance as the currency or measure that is being minimized. We recognize that distance may not be the only measure for efficiency and that the travelers might be sensitive to other currencies not reported here (e.g., time, momentum). The number of possible one-way routes or solutions that could be constructed for a given problem is defined by the equation $S = n!$, where S is the number of solutions and n is the number of nodes in a problem. Thus, for a problem with three nodes, there are six possible solutions ($3! = 6$). Given the three-node problem in Figure 1 (top row), the participant could select Node c first and then Node b, followed by Node a; the result would be a total distance traveled of 25 cm, which is the shortest of all possible routes for this problem. If the participant selected Node b first, then Node a, and finally Node c (see Figure 1, middle row), then the total length of the route would be 30 cm, which is 5 cm longer than the most efficient solution. A participant could also select Node a, followed by Node c, and finally Node b; such a route would have a length of 45 cm. Three additional routes are possible by reversing the sequence of the nodes taken along the three routes defined above, but these three routes would have the same total lengths as the first three. We defined the number of possible routes for a given traveling problem by the number of routes that led to a unique route length ($S = n!/2$). Thus, a problem with three nodes would have three routes. A participant that selected Route b, a, c may be doing something very different (e.g., selecting two close nodes first) than a participant who selected Route c, a, b, even though they have the same route length. This aspect of route selection was addressed by another set of analyses described below.

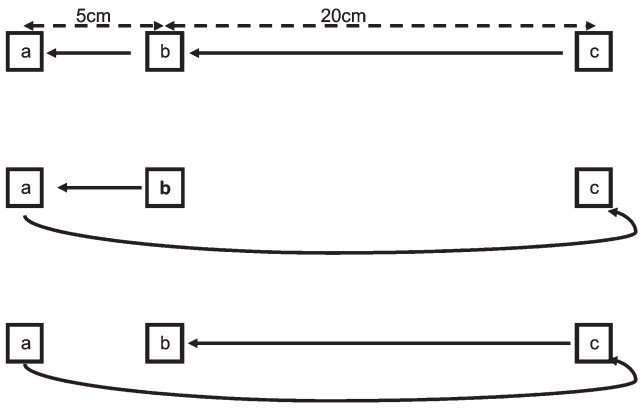

Figure 1. A potential three-node problem in Experiment 1. The arrows indicate three potential one-way routes for a problem with three nodes (a, b, c). Dashed arrows at the top indicate the distances between the nodes in this example.

The three-node problem in Figure 1 is an extreme case, in which the differences among the three solutions, and correspondingly the differences in the route lengths among the three solutions, are relatively large. Detecting which solutions would be most efficient and minimizing the distance of the route may be relatively simple in this case. At the other extreme is a problem in which the three nodes are positioned near the corners of an equilateral triangle. In this case, all three solutions would have nearly the same length; it should be more difficult to determine which of the three solutions has the shortest route length. Between these extremes are the infinite configurations of arrays of traveling problems with three nodes. Arrays that are more "linear" have solutions that are more variable in path length, whereas arrays that are more equilateral or uniform generally have solutions and path lengths that are more similar to each other.

One important feature of the current experimental design was that each participant encountered a different configuration of nodes on each trial; thus, the problem set and solutions that each participant encountered were unique. We developed a measure of *solution disparity* that quantified the degree of difference in path length among the solutions for a given problem as a potential index of problem "difficulty." The solution disparity index allowed us to better compare problems with the same number of nodes but with different configurations and dimensions. The solution disparity measure was calculated for each problem by taking the mean path length of all possible solutions for a given problem and dividing it by the standard deviation of the solutions for the same problem; we then divided 1.00 by this value. As the difference in the total distance of two or more solutions increases, the solution disparity score also increases; conversely, as the potential routes of a problem become less discernable, the solution disparity score decreases. Finally, although for simplicity much of this discussion has been based on examples with three nodes, the basic principles regarding the routes and the determination of solution disparity also apply to problems with four and five nodes.

We constructed three models of performance; these models encountered the same traveling problems as the participants. The first was a Monte Carlo simulation or a random model of performance. For each problem that a participant encountered, a computer randomly selected each node once, and the

order in which the nodes were selected was always according to a random function. Thus, this model encountered each problem once per trial like the people. We also constructed a nearest neighbor model of performance. For each problem, the computer determined the identity of the node that the participant had selected first. The computer then was programmed to choose the next closest node in the problem, thereby generating the first leg of the nearest neighbor route. It is important to note that the computer continued to choose unselected nodes using the nearest neighbor rule until all of the available nodes in a problem (correspondingly all node-to-node transitions) were selected once. The third was an optimal traveler model; for this model, the computer selected the shortest possible route for each problem.

For each problem in each session, we recorded the length of the route selected by the participant and the solution disparity score. The disparity scores were then ranked from highest to lowest and sorted into quartiles (30 scores per quartile; the highest 25% of scores, the most discernable solutions, were in Quartile 1); the path lengths associated with the disparity scores in each quartile were averaged for each session and across sessions. We then conducted three mixed-factor analyses of variance (ANOVAs), one each for the data sets with three, four, and five nodes. Each ANOVA used route distance as a dependent measure, traveler (human participant, Monte Carlo, nearest neighbor, optimal) as a between-groups factor and solution disparity (Quartiles 1–4) as a repeated measure. Alpha was set to $p < .05$ for the determination of significant effects.

It is possible that the participants selected "clusters" of nodes that were spaced closely together before moving to other nodes that were positioned farther apart. To examine this possibility, we calculated the distance between all possible combinations of two nodes (a leg) in a problem and rank ordered them from shortest (rank = 1) to longest. If the participants selected nodes that were clustered in the beginning of a trial, then the proportion of trials on which they selected a leg with the highest ranking (i.e., shortest internode distance) as the first leg of a route should have been higher on average than the proportion of trials on which a Monte Carlo model (given the same problems) would have selected the shortest leg as the initial leg of a trip. Note that the cluster analysis and comparisons of the participant's performance with the nearest neighbor model, mentioned above, analyze different aspects of the participant's behavior and are mutually exclusive. For example, if a participant's route was identical to that shown in the top row of Figure 1, she would score high on comparisons with the nearest neighbor model, but she would score low on the cluster analysis. If, however, the route that the participant took was in the reverse direction from the one shown in the top row of Figure 1, then the cluster and nearest neighbor analysis would indicate a similar initial trend. In this case, we can only indicate a similar "initial trend" because the nearest neighbor analysis goes on to compare all leg choices in the route, whereas the cluster analysis considers only the participant's first choice. We conducted three mixed-factor ANOVAs, one for problems with three, four, and five nodes. For each ANOVA, we used the proportion of trials that a leg was selected as the first leg of a trip as a dependent measure, with traveler (human participant, Monte Carlo) as a between-groups factor and the number of possible leg rankings for a problem (3 for problems with three nodes, 6 for problems with four nodes, and 10 for problems with five nodes) as a repeated measure.

Finally, to see whether the participants' routes were similar to those consistent with the nearest neighbor model, we calculated the proportion of routes the people selected that corresponded to the route that was selected by the nearest neighbor model (as detailed above). This analysis included all of the choices made by the participants.

Results

ANOVA results indicated a reliable effect of traveler for problems with three nodes, $F(3, 68) = 225.07$. Planned pairwise comparisons indicated that the mean distance of the routes selected by the human participants was significantly shorter (see Figure 2, top panel) than those selected by the Monte Carlo model and significantly longer than the minimum route (ps $< .05$). Notably, the routes selected by the human participants did not differ in length from those selected by the nearest neighbor model ($p > .05$). ANOVA results also indicated a reliable interaction between traveler and solution disparity, $F(9, 204) = 7.11$ (see Figure 3, top panel). Follow-up comparisons indicated that the routes selected by the participants were reliably shorter than those selected by the Monte Carlo model and reliably longer than those of the optimal model at all four levels of solution disparity (ps $< .05$). The routes selected by people were not significantly different in length from those selected by the nearest neighbor at all four levels of solution disparity (ps $> .05$).

A similar pattern of results was observed for the problems that contained four nodes (see Figure 2, middle panel). Again, ANOVA results indicated a significant effect of traveler, $F(3, 68) = 218.96$. Pairwise comparisons revealed that the routes selected by the participants were shorter than those selected by the Monte Carlo model but significantly longer than those of the optimal route (ps $< .05$). There was no difference in the length of the routes selected by the people and the nearest neighbor model ($p > .05$). There was an interaction between traveler and solution disparity, $F(9, 204) = 12.55$ (see Figure 3, middle panel). Follow-up comparisons indicated that, at all four levels of solution disparity, the routes people selected were reliably shorter than those selected by the Monte Carlo model and reliably longer than the minimum route (ps $< .05$). The routes selected by people were not different in length compared with those selected by the nearest neighbor at all four levels of solution disparity (ps $> .05$).

The pattern of results for human participants was somewhat different for problems with five nodes from those patterns observed when three or four nodes were included in the problem set (see Figure 2, bottom panel). As with the analyses for three and four nodes, ANOVA results indicated a significant effect of traveler, $F(3, 68) = 162.37$. Again, pairwise comparisons revealed that the routes selected by human participants were shorter than those selected by the Monte Carlo model but significantly longer than those of the nearest neighbor model and the minimum route (ps $< .05$). There was an interaction between traveler and solution disparity, $F(9, 204) = 12.55$ (see Figure 3, bottom panel). Follow-up comparisons indicated that, at all four levels of solution disparity, the routes people selected were reliably shorter than those selected by the Monte Carlo model and reliably longer than the minimum route (ps $< .05$). The routes selected by the people were no different in length from those selected by the nearest neighbor model for the first two levels of solution disparity (ps $> .05$),

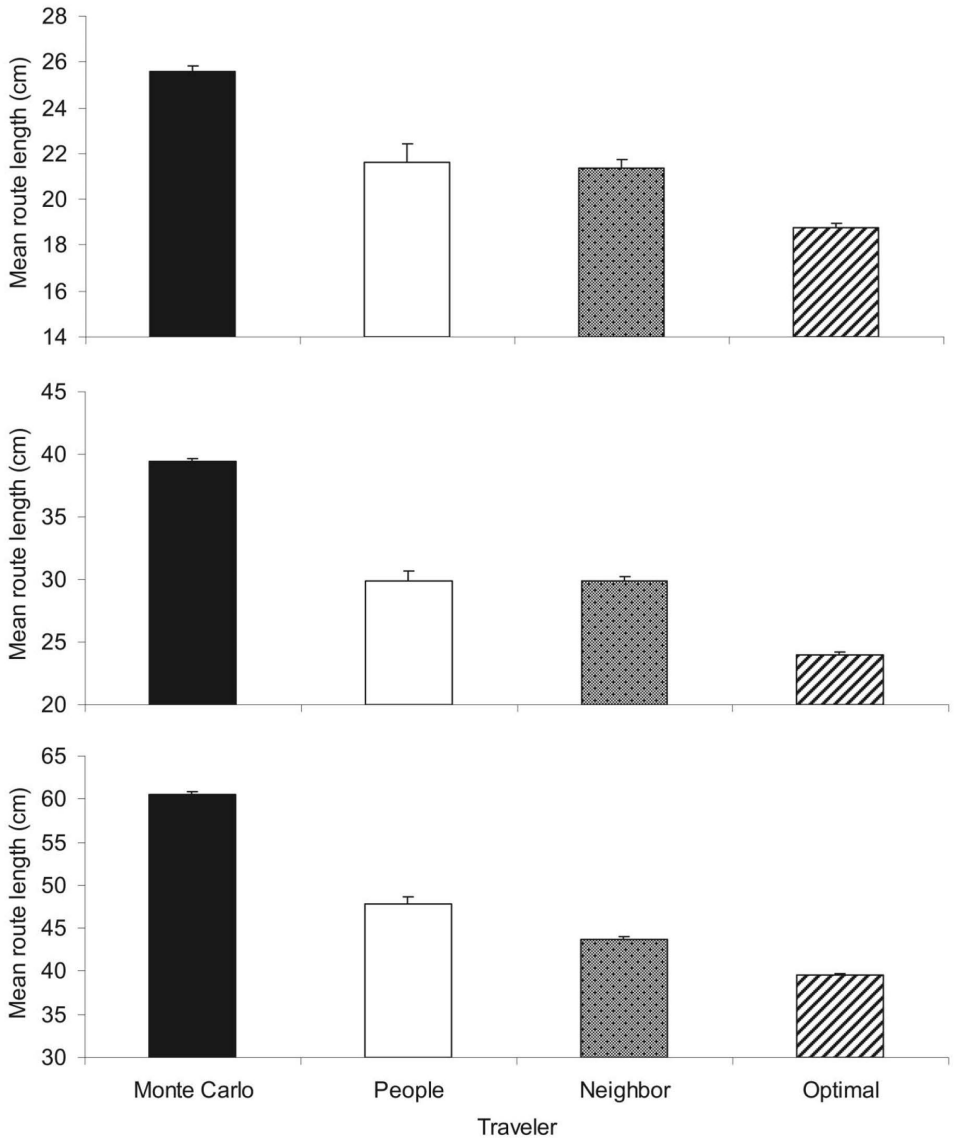

Figure 2. The mean length of the routes selected by the Monte Carlo model, people, the nearest neighbor model, and the optimal model for problems with three nodes (top), four nodes (middle), and five nodes (bottom). Vertical lines depict standard errors of the means.

but they were significantly longer than those routes selected by the nearest neighbor model for the last two quartiles of solution disparity (*p*s < .05).

ANOVA results from the cluster analysis revealed a significant interaction with three nodes between leg and traveler, $F(2, 68) = 50.75$. Follow-up comparisons indicated that people tended to overselect the shortest leg, $t(1, 34) = 7.31$, and to underselect the longest leg of a problem to be used as the first leg of the trip, $t(1, 34) = 10.90$, compared with the Monte Carlo model (see Figure 4, top panel). The same pattern was observed for problems with four nodes (see Figure 4, middle panel). ANOVA results indicated a significant interaction between leg and traveler, $F(5, 170) = 30.74$. Follow-up comparisons indicated that people overselected the shortest two legs (Legs 1 and 2) and underselected the longest two legs (Legs 5 and 6) to be used as the first leg of the trip (all *p*s < .05). Notably, there was also a significant interaction between leg and traveler for problems with five nodes, $F(9, 306) = 28.76$. The participants overselected the shortest three legs and underselected the longest four legs as the first leg of the route (all *p*s < .05).

One concern might be that the error variance for the participants was somewhat greater than that observed for the models and might violate the statistical assumptions of the ANOVAs used to examine for reliable differences between groups. To this end, we conducted Levene's test of equality of error variances for each analysis reported above. In no case did the Levene's test indicate that there was a significant difference in error variances for any of the groups (all *p*s > .05).

In an attempt to determine what, if any, systematic approaches people were using to efficiently solve the TSPs, we calculated the proportion of the participants' routes that conformed to those taken by the nearest neighbor model. A nearest neighbor route can be an efficient way to solve a TSP, and the people might have taken such routes to minimize the dis-

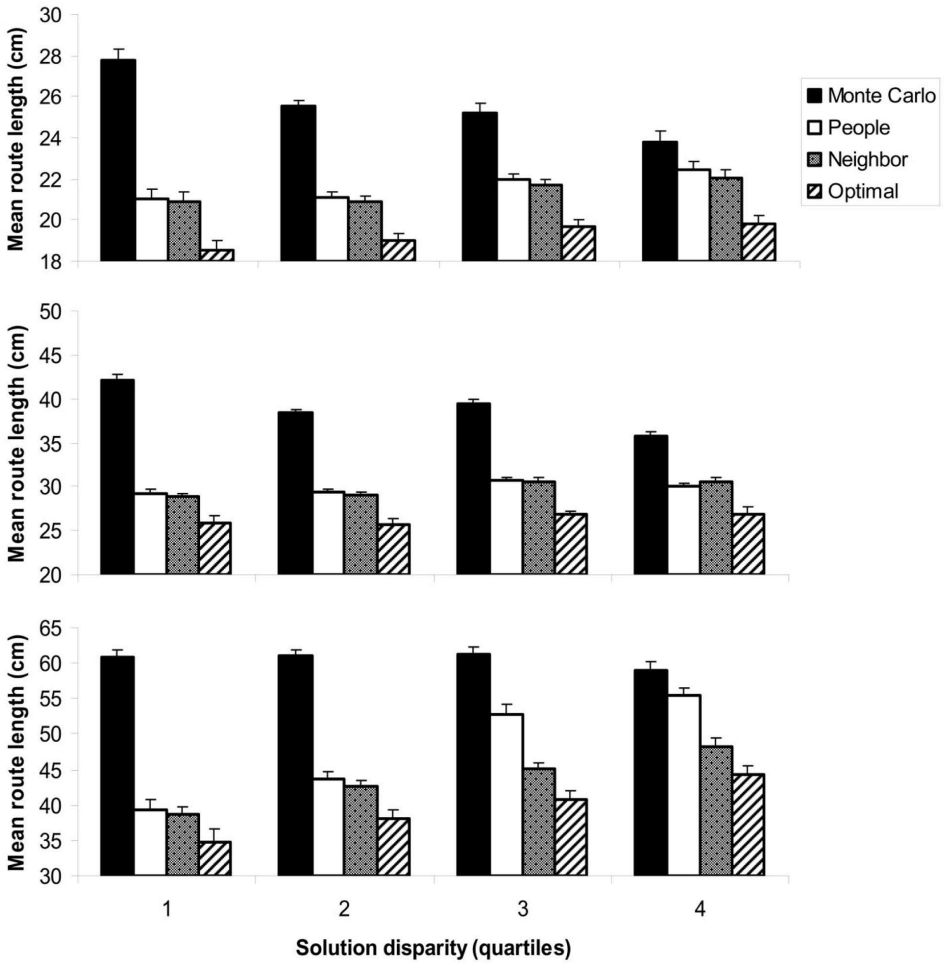

Figure 3. The mean length of the routes selected by the Monte Carlo model, people, the nearest neighbor model, and the optimal model for problems with three nodes (top), four nodes (middle), and five nodes (bottom) across decreasing levels of solution disparity. Vertical lines depict standard errors of the means.

tance traveled. The proportions of routes that were identical to the nearest neighbor model were $M = 0.82$, $SEM = 0.05$, for problems with three nodes; $M = 0.78$, $SEM = 0.05$, for problems with four nodes; and $M = 0.67$, $SEM = 0.09$, for problems with five nodes.

Discussion

The mean length of the participants' routes was reliably shorter than that selected by the Monte Carlo model but longer than those routes selected by the optimal model. Although participants' performance was less than optimal, the mean length of their routes was comparable to those selected by the nearest neighbor model of performance (although this characterization is not true for problems with five nodes in the last two quartiles). Indeed, the participants selected the route consistent with the nearest neighbor model on 76% of the trials (across problems with three, four, and five nodes).

The results of the current experiment are somewhat different from those that have been reported previously for human participants solving TSPs. MacGregor and Ormerod (1996) presented human participants with six TSPs with 10 nodes and seven TSPs with 20 nodes individually on sheets of paper. The participants were required to solve the problems by connecting the nodes with a pen. Subsequent analysis indicated that the participants' solutions were very close to optimal and notably better than those selected by the nearest neighbor model. There are several procedural differences between the current study and the experiments by MacGregor and Ormerod that may account for these differences in performance. The most obvious difference is that the participants in MacGregor and Ormerod's study drew lines to connect each of the nodes in a problem. Because these lines remained on the paper, the participants' need to recall whether or not they had previously visited a node may have been reduced, thereby increasing route efficiency. In addition, our participants were not required to make a complete round trip using all of the nodes, as was required for the participants in the study conducted by MacGregor and Ormerod. The TSPs presented by MacGregor and Ormerod included many more nodes than those used in the current experiment, which may have encouraged different types of solutions. Another difference may be that the problems in our study were presented in the vertical plane on a computer display, whereas the participants in the MacGregor and Ormerod study were given problems on sheets of paper resting on a tabletop.

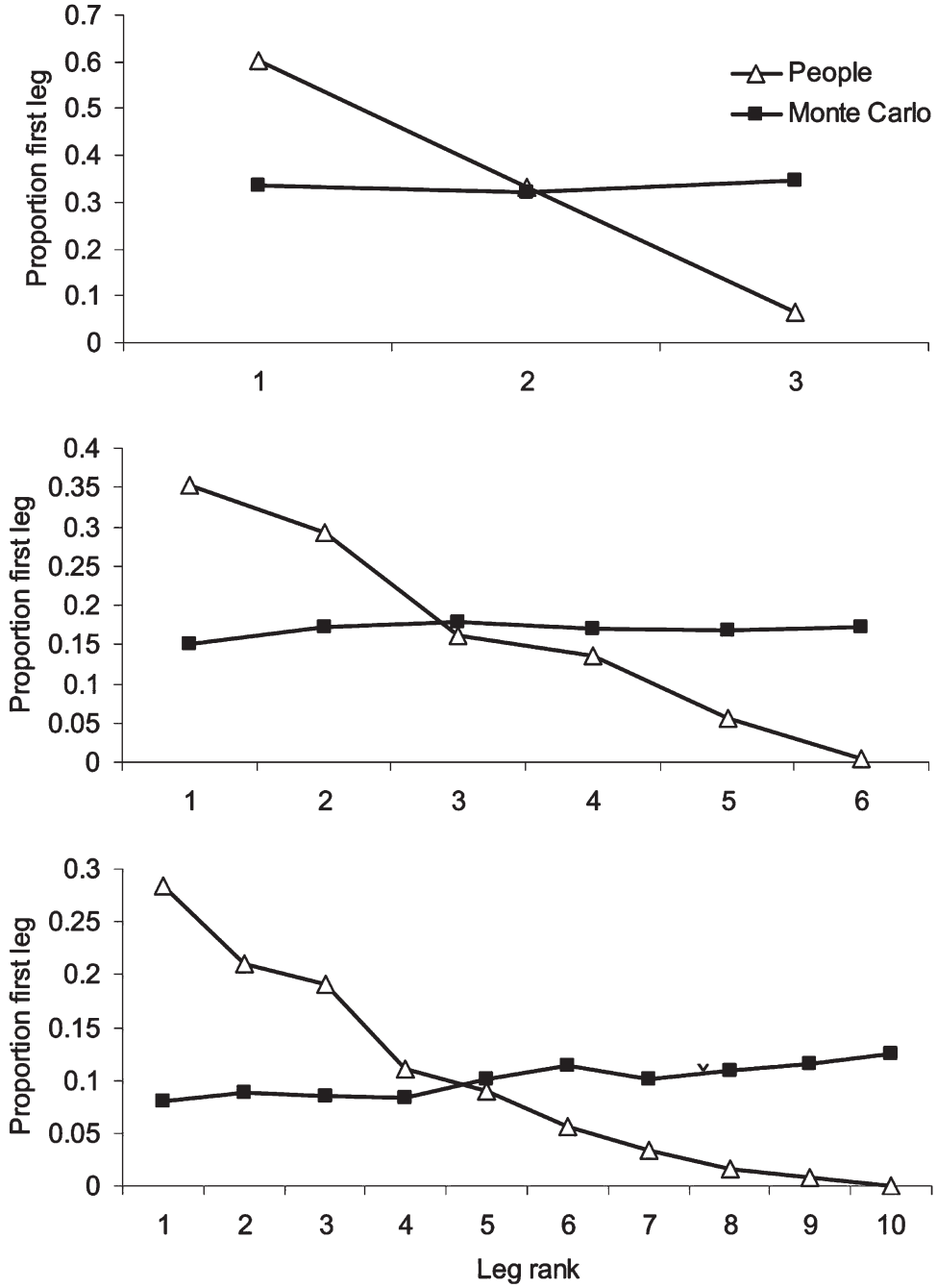

Figure 4. The proportion of trials that each possible leg of a problem was selected as the first leg of a route by people for problems with three nodes (top), four nodes (middle), and five nodes (bottom). The possible legs of a problem are rank ordered on the x-axis from shortest (left) to lon-

Experiment 2

In Experiment 2, we investigated pigeons' ability to solve TSPs with three, four, and five nodes in an operant chamber. Testing the pigeons in an operant chamber provided us with the opportunity to deliver a large number of TSPs and to evaluate performance. On each trial, a unique configuration of routes appeared on the video display in the chamber, as was the case with human participants in Experiment 1. The pigeons were required to peck each node once without returning to a previously visited node. Completion of the problem resulted in the delivery of food, whereas a revisit to any node during the trial resulted in a correction trial. The birds completed 120 problems during the course of a daily session. Afterward, the birds' choices were used to determine the route they had taken. As in Experiment 1, the route then was compared with different models of performance (e.g., Monte Carlo, nearest neighbor, optimal). Subsequent analyses were conducted to examine possible regularities in the way the pigeons solved the TSPs. To our knowledge, this is the first time that a TSP has been given to a nonhuman animal in an operant environment.

Method

Animals. Four adult pigeons (*Columba livia*) were studied. The pigeons were kept at 85% of their free-feeding weight by controlled feedings of mixed grain given after daily experimental sessions. The birds had free access to grit and water that contained a vitamin supplement.

Apparatus. Training and testing were conducted in operant chambers. A 15-in. high-resolution LCD monitor (the same as that used in Experiment 1) was fitted into the front wall of the operant chamber. A touchscreen (Model E14603-000; Elo TouchSystems, Fremont, CA) overlaid the face of the monitor and was used to record the Cartesian location of the birds' responses (pecks) to the nodes of each TSP presented on the display. Food pellets (45-mg; Research Diets, Inc., New Brunswick, NJ) were dispensed into a small cup located on the floor next to the rear wall of the chamber.

Training. Each of the birds was initially shaped to peck at a colored square (side = 7 cm) that appeared in the center of the monitor. We then reduced the size of the square from 7 × 7 cm to 2 × 2 cm. Next, the global position of the square on the computer monitor was varied from trial to trial, so that each bird was familiarized with pecking at stimuli that could appear anywhere on the screen. The square was not positioned closer than 2 cm to the perimeter of the display area.

Experimental training began after this initial period of shaping. The start stimulus, as described in Experiment 1, appeared in the center of the screen to signal the onset of each trial. A peck to the start stimulus was required to advance the trial; a single node (as described in Experiment 1) then appeared on the screen. As in Experiment 1, the position of the node was randomly determined prior to the start of a trial. A single response to the node caused it to become shaded, providing a cue to the bird that it had responded to the stimulus. The display then was cleared from the screen, and two food pellets were delivered; the next trial began following a 15-s intertrial interval. Each daily session comprised 120 trials, and training continued until the bird successfully responded to the stimulus on every trial.

We then presented the bird with two nodes (identical to those described above) on the computer screen during each trial of the next stage of training. The position of each node was determined randomly prior to the start of each trial with the constraint that the nodes could not be closer than 6 cm (center to center). The bird was required to peck each node once; as each node was pecked, it was shaded as previously described. After the second node was pecked, the stimulus array was cleared from the screen, and two food pellets were delivered into the chamber; the next trial began following a 15-s intertrial interval. Each daily session again consisted of 120 trials, and the birds continued this training until they successfully completed all 120 trials.

Testing. We presented the birds with arrays of three nodes, as this was the minimum number that would be required for a traveling problem (i.e., with two nodes, there is only one route that can be taken in either direction: A→B or A←B). The procedures for these trials were nearly identical to those described for Experiment 1 and are only briefly summarized here. On each trial, the bird was presented with an array of three copies of the square stimulus that was previously described for training. A bird could select any of the three nodes as the starting node; it was then required to respond to the two remaining nodes just once without returning to a node that had been previously pecked. A return or response to a previously pecked node resulted in all of the nodes being immediately cleared from the screen and the houselight being turned off for a 30-s timeout. As in Experiment 1, each pigeon received different TSPs on each trial of a session. Each daily session of testing consisted of 120 such problems or trials, and testing with three nodes in a problem continued for 12 days. Following completion of testing with three nodes, we conducted a block of 12 sessions in which problems with four nodes were exclusively presented and then a final block of 12 sessions in which problems with five nodes were presented. The sequence of events during these sessions was otherwise identical to that described for testing with three nodes.

Measures and analyses. The measures and the analyses were identical to those described for Experiment 1.

Results

The mean lengths of the routes selected by the pigeons, the Monte Carlo model, the nearest neighbor model, and the optimal model for problems having three nodes are displayed in Figure 5 (top). The mean distances of the routes selected by pigeons across all problems with three nodes were shorter than those for the Monte Carlo model but longer than those selected by the nearest neighbor and optimal models. Correspondingly, ANOVA results revealed a significant main effect of traveler, $F(3, 12) = 682.02$; planned pairwise comparisons indicated that the lengths of the routes selected by the pigeons were reliably shorter than those of the Monte Carlo model but longer than those of the nearest neighbor and optimal models (all ps < .05).

The mean distance of the routes selected by the Monte Carlo model became shorter and the mean distance of the routes selected by the nearest neighbor model became somewhat longer with decreasing solution disparity (see Figure 6, top panel). The mean distance of the routes selected by the pigeons, however, remained relatively unchanged across all levels of solution disparity. Correspondingly, ANOVA results revealed a significant interaction between traveler and solution disparity, $F(9, 36) = 22.90$. Follow-up Bonferroni comparisons indicated that the lengths of the routes selected by the pigeons were significantly shorter than those of the Monte Carlo model for each of the first three quartiles of solution disparity (ps < .05) but significantly longer than those of the nearest neighbor model for all four levels of solution disparity (all ps < .05). The analysis also indicated a significant main effect of solution disparity, $F(3, 36) = 27.34$.

A similar pattern was observed for the block of sessions with four nodes in each problem (see Figure 5, middle panel). The mean distance of all of the routes selected by the pigeons was shorter than that of the Monte Carlo model but longer than that of the nearest neighbor and optimal models. ANOVA results again indicated a reliable effect of traveler, $F(3, 12) = 353.62$; planned pairwise comparisons indicated that the routes selected by the pigeons were shorter than those of the Monte Carlo model but longer than those selected by the nearest neighbor and optimal models (all ps < .05). The mean distances of the routes selected by the pigeons and the three models again were most divergent for problems that had the greatest solution disparity (see Figure 6, middle panel) but converged as the solution disparity decreased. ANOVA results

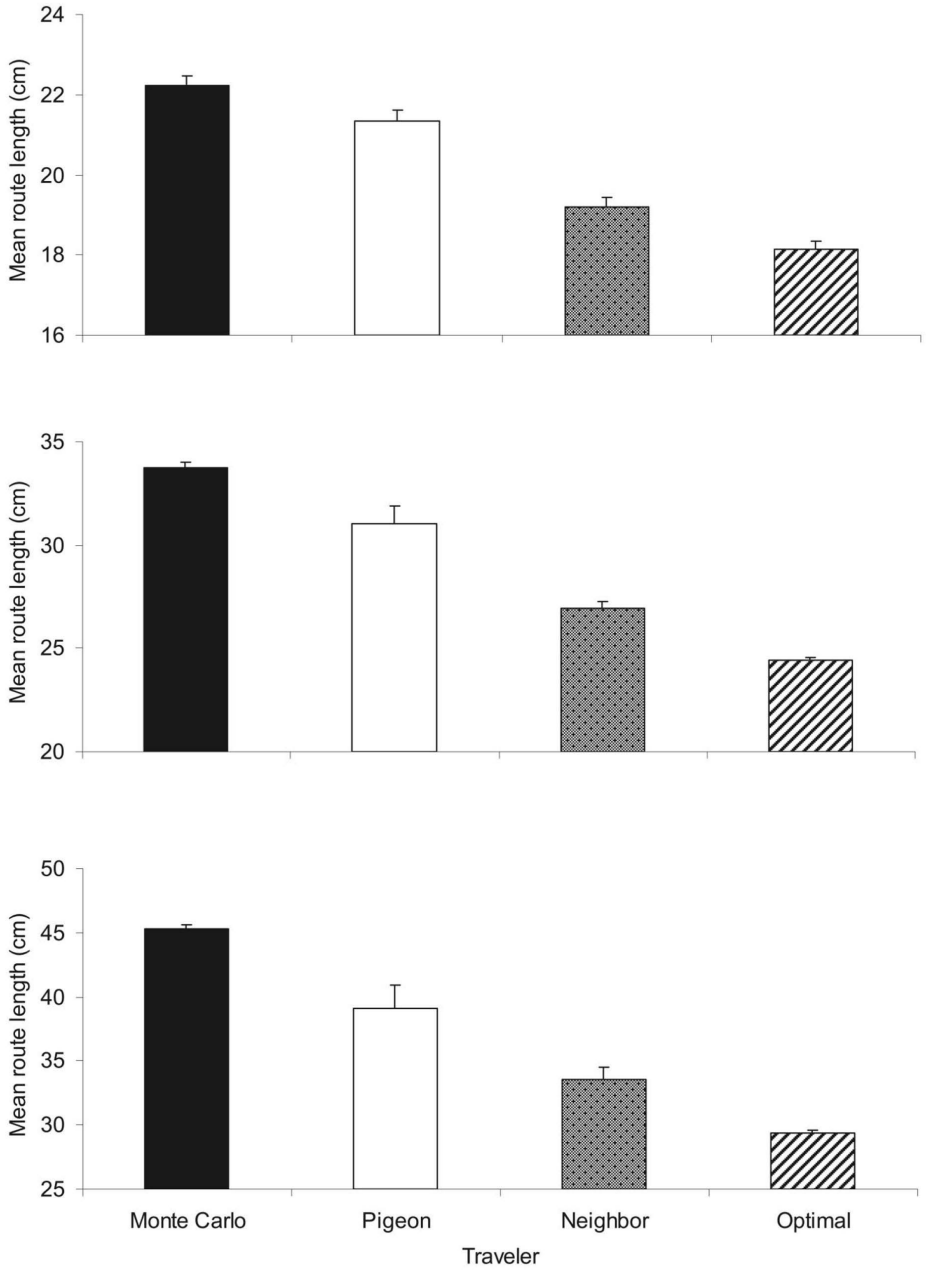

Figure 5. The mean length of the routes selected by the Monte Carlo model, pigeons, the nearest neighbor model, and the optimal model for problems with three nodes (top), four nodes (middle), and five nodes (bottom). Vertical lines depict standard errors of the means.

indicated a reliable interaction between the traveler and solution disparity variables, $F(9, 36) = 86.82$. Follow-up Bonferroni comparisons indicated that the mean distance of the routes selected by the pigeons was significantly shorter than that of the Monte Carlo model but significantly longer than that of the nearest neighbor model for each of the four levels of solution disparity (ps < .05). Again, ANOVA results revealed a significant main effect of solution disparity, $F(3, 36) = 12.11$.

The results for the problems with five nodes were similar to those with three and four nodes. The lengths of the pigeons' routes were shorter than those expected by chance but longer than those of the nearest neighbor or optimal models (see Figure 5, bottom panel). An ANOVA indicated that the effect of traveler was significant, $F(3, 12) = 199.79$; subsequent pairwise comparisons revealed that the routes that the pigeons selected were shorter than those expected by chance (Monte Carlo) but longer than those for the nearest neighbor or optimal models (ps < .05). The mean distance of the pigeons' solutions remained stable as the solution disparity decreased, whereas the mean distance of the routes selected by the other three travelers converged somewhat as the solution disparity decreased (see Figure 6, bottom panel). Correspondingly, there was a reliable interaction between the type of traveler and solution disparity, $F(9, 36) = 30.75$. Follow-up comparisons indicated that

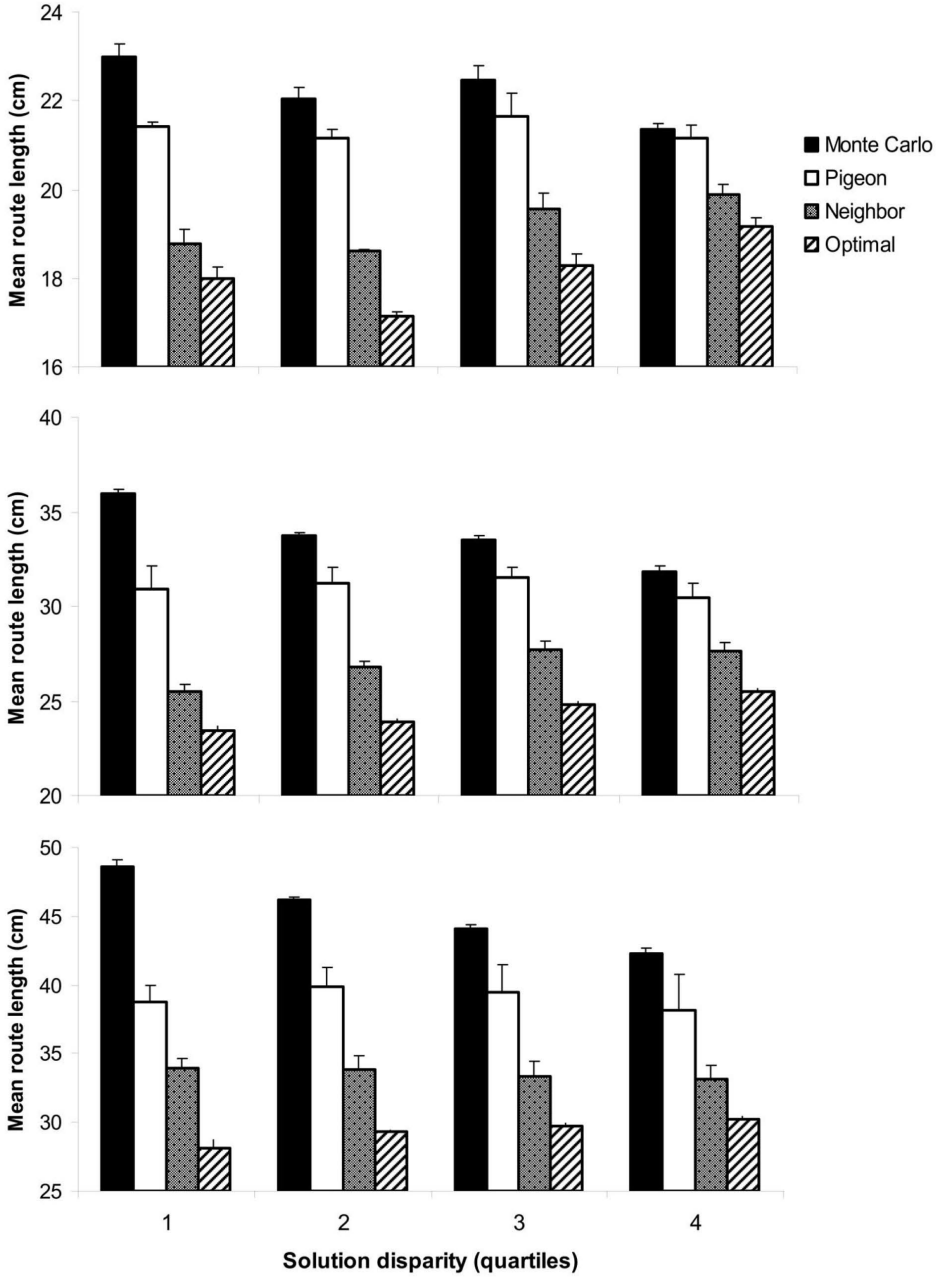

Figure 6. The mean length of the routes selected by the Monte Carlo model, pigeons, the nearest neighbor model, and the optimal model for problems with three nodes (top), four nodes (middle), and five nodes (bottom) across decreasing levels of solution disparity. Vertical lines depict standard errors of the means.

the routes selected by the pigeons were reliably shorter than those routes selected at random (Monte Carlo) but longer than those of the nearest neighbor model for each level of solution disparity (*p*s < .05). ANOVA results indicated a main effect of solution disparity, $F(3, 36) = 32.04$. Levene's tests for all of the statistical comparisons reported above failed to indicate a significant difference in error variances for any of the groups (all *p*s < .05).

The pigeons tended to select the shortest possible leg (rank = 1) and were less likely to select the longest leg (rank = 3) as the first leg of their route for problems with three nodes (see Figure 7, top panel). ANOVA results indicated a significant main effect of leg rank, $F(2, 12) = 40.03$, as well as an interaction between leg rank and traveler, $F(2, 12) = 40.03$. Follow-up comparisons indicated that the pigeons had a larger proportion of legs with the lowest rank as the first leg of their route compared with the Monte Carlo model. Similarly, compared with the Monte Carlo model, pigeons also included fewer legs with the highest rank as the first leg of their trip (*p*s < .05).

A similar pattern was observed for problems with four nodes. The pigeons were more likely to include either of the shortest two legs of a problem and less likely to include ei-

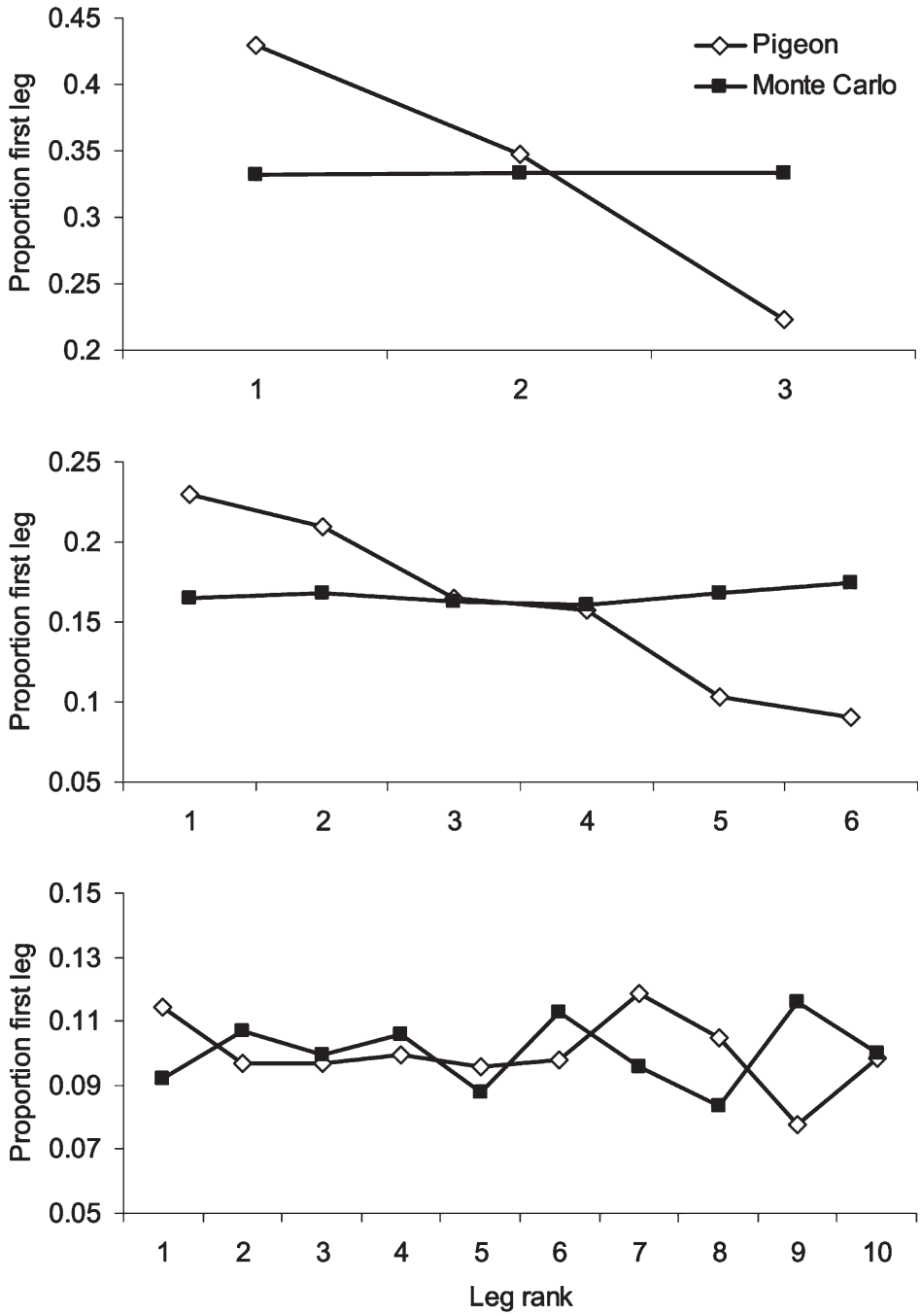

Figure 7. The proportion of trials that each possible leg of a problem was selected as the first leg of a route by pigeons for problems with three nodes (top), four nodes (middle), and five nodes (bottom). The possible legs of a problem are rank ordered on the x-axis from shortest (left) to longest (right).

ther of the longest two legs of a problem as the first leg of their trip compared with the Monte Carlo model (see Figure 7, middle panel). ANOVA results again revealed a reliable interaction between leg rank and traveler, $F(5, 30) = 34.47$. Follow-up comparisons exploring this interaction indicated that the pigeons were more likely to select either of the two shortest legs of a problem as their first leg and less likely to select the longest two legs of the problem compared with the Monte Carlo model (all ps < .05). The main effect of leg rank was significant, $F(5, 30) = 31.10$, and there was no overall difference between the pigeons and Monte Carlo model, $F(1, 6) = 0.27$.

Notably, the pigeons and the Monte Carlo model selected a similar proportion of the 10 possible legs as the first leg of their trip for problems with five nodes, as the effect of traveler, $F(3, 54) = 2.58$, was not significant (see Figure 7, bottom panel). There was a significant interaction between traveler and leg rank, $F(9, 54) = 2.58$, however, as the pigeons selected more legs with ranks of 1, 7, and 8 compared with the Monte Carlo

model but fewer legs with a rank of 9 as the first leg of their trip (ps < .05). The effect of leg, $F(9, 54) = 2.48$, was significant.

In an additional attempt to characterize any regularities in the way that the pigeons may have solved the TSPs, we calculated the proportion of the pigeons' routes that conformed to the route taken by the nearest neighbor model (considering all node choices during a trial). As mentioned above, the nearest neighbor model can be a relatively efficient method of solving a TSP. The proportions of the pigeons' routes that were identical to the nearest neighbor model were $M = 0.35$, $SEM = 0.03$, for problems with three nodes; $M = 0.31$, $SEM = 0.01$, for problems with four nodes; and $M = 0.33$, $SEM = 0.04$, for problems with five nodes in Experiment 2.

Discussion

The mean distance of the routes selected by the pigeons was reliably shorter than the mean distances of the routes selected by the Monte Carlo model for problems with three, four, and five nodes. Thus, the pigeons were not randomly pecking the nodes to complete each problem. This finding is impressive considering the diverse population of problems the pigeons were given. The finding is consistent with other work indicating that primates will select an efficient route when faced with multiple route alternatives (e.g., Gallistel & Cramer, 1996; MacDonald, 1994).

When the solution disparity was high for problems with three, four, and five nodes—that is, when the difference in distance between the solutions to the problems was large—the difference in the distance of the routes selected by the Monte Carlo model and the pigeons was large. This finding can be attributed to the fact that the Monte Carlo model occasionally selected the longest of the possible routes for a given problem, whereas the pigeons rarely made such selections. On the other hand, the pigeons were not so efficient as to always select the shortest routes; the difference between the pigeons and the nearest neighbor and optimal models was also quite large. As the solution disparity decreased, the mean distance of the routes selected by the Monte Carlo model generally decreased, and the distance of the routes selected by the nearest neighbor and optimal models increased. Notably, the mean distance of the routes selected by the pigeons tended to stay the same as the solution disparity decreased. This pattern of results suggests that the way in which the pigeons solved the TSPs remained efficient, despite the increasing difficulty of the problems.

Another notable finding is that the pigeons appeared to be more efficient when the problems contained more nodes. Specifically, the difference in the distance of the routes selected by the pigeons and the Monte Carlo model increased as the number of nodes in the problems increased from three to five (see Figure 5). Using the data presented in Figure 5, the difference between the routes selected by the pigeons and the Monte Carlo model was 4% of the total length of the Monte Carlo route for problems with three nodes (distance Monte Carlo – distance pigeon/distance Monte Carlo), 8% for problems with four nodes, and 14% for problems with five nodes. Again, the pigeons did a relatively good job of avoiding routes that were excessively long compared with the Monte Carlo model; this trend became more apparent as the number of nodes, and the potential for selecting a relatively inefficient route, increased.

The improvement in performance with increasing number of nodes was, of course, confounded by the fact that pigeons were gaining more experience with traveling problems. Still, if repeated exposure to traveling problems alone accounted for the improvement in performance, then the improvement might have been expected to occur steadily across sessions of problems with the same number of nodes, rather than more abruptly across problems with increasing number of nodes. Yet, the mean distance of the routes selected by the pigeons was comparable across sessions with a given number of nodes (data not shown).

Were the pigeons using a definable heuristic to solve the traveling problems? It is possible that the pigeons considered which leg they should select first from the various legs that could be selected in a given problem. The pigeons had a greater tendency to select the shortest legs and to avoid the longest legs of a problem as the first leg of their route. The tendency of the pigeons to initially seek the shortest leg of the trip is consistent with other work indicating that primates given similar types of problems will try to travel to clusters of nodes before moving to nodes that are spaced farther apart (Janson, 1998). This finding also suggests that the pigeons examined large portions or perhaps the entire problem, seeking clusters of nodes before selecting a route, particularly for problems with three or four nodes.

Although there was some tendency for the birds to select the shortest leg first for problems with five nodes, the overall pattern of selecting the shortest legs and avoiding the longest legs when making their first choice was not as clear here as was the case for problems with three and four nodes and may represent a shift in the way the pigeons solved these problems. Yet, as reported above, the pigeons actually selected more efficient routes than the Monte Carlo model for problems that included five nodes compared with problems that included three or four nodes. Obviously, there are a number of efficient routes for a given problem that do not require selecting the shortest initial leg of a problem. For example, a pigeon could have selected the route in the top panel of Figure 1 in either direction and still have arrived at the most efficient route.

Although pigeons tended to select the shortest leg of the problem as the first leg of their route (particularly for problems with three and four nodes), they were not choosing the next node in the route on the basis of the nearest neighbor model. The mean distance of the routes selected by the pigeons was far in excess of those routes selected by the nearest neighbor model given identical problems. Likewise, only about a third of the pigeons' routes were identical to those selected by the nearest neighbor model (across problems with different numbers of nodes).

The mean length of the problems presented to the human participants in Experiment 1 was somewhat longer than that for the pigeons (optimal routes; see Figures 2 and 5) in the current experiment. This is to be expected, as the human participants received a smaller sample of problems. The pattern of results for the Monte Carlo, nearest neighbor, and optimal models was similar for the sets of problems given to people and pigeons, suggesting that the problems each encountered were qualitatively similar. Both people and pigeons were significantly more efficient than the Monte Carlo model, but they were less efficient than the optimal model. The mean length of the routes selected by the human participants was no different from that selected by the nearest neighbor model, whereas the pigeons' routes were significantly longer than those se-

lected by the nearest neighbor model. The proportion of solutions that matched the nearest neighbor model was also substantially higher for people than for the pigeons. Notably, both people and pigeons tended to use the shortest legs of the problem as the first leg of the route, and, correspondingly, both tended to avoid using the longest legs in this position.

Experiment 3

The results of Experiment 2 indicated that the pigeons exhibited significantly shorter routes than expected by chance for traveling problems with three, four, and five nodes. Although the pigeons' routes were significantly shorter than those expected by chance, they were reliably longer than those of the nearest neighbor model and far below optimal. The cost of selecting an inefficient route (presumably the time until the delivery of food) in Experiment 2 would appear to be relatively small and may account for why the pigeons selected longer routes on some trials. Presumably, the limited costs that were encountered had some effect in Experiment 2, otherwise the birds' performance may not have been better than chance.

In Experiment 3, we attempted to improve the efficiency of the routes selected by the pigeons by requiring that their routes meet a minimum standard of performance (criterion). Pigeons, whose routes fell below the performance criterion, were required to repeat the trial (problem) until they had selected a route that met the minimum standard of efficiency.

Method

Animals and apparatus. The animals and apparatus were the same as those used in Experiment 2.

Procedure. The general procedures for Experiment 3 were similar to those used in Experiment 2. One difference was that all of the problems the pigeons encountered in Experiment 3 contained four nodes. A second difference was that the route a pigeon selected during the course of a trial was evaluated to determine whether it met a criterion for efficiency. Specifically, for traveling problems with four nodes, there are 12 unique routes (see *Method* in Experiment 1) that could be selected. For each trial in Experiment 3, we rank ordered these routes from highest to lowest, so that a rank of 1 was given to a route that had the shortest possible length, and a rank of 12 was given to a route that had the longest possible length. The pigeons were required to select a route whose solution was greater or equal to that of the criterion before continuing to the next trial. If the route that the pigeon selected during the first pass through the trial did not meet or exceed the criterion, then the stimuli disappeared from the screen, and the pigeon was required to wait for 30 s; the same configuration of four nodes then reappeared on the screen. The pigeon was required to repeat the trial until the route that it had selected was equal to or lower than the criterion for performance. For example, if the pigeon selected a route that had a rank of 6 of 12, then its solution would be in the top 50% of all possible routes. If the criterion required that the route be in the top 66% of all solutions—a rank of 4 or higher of 12—then the pigeon would be required to repeat the trial with the same problem until it selected a route that was at or higher than the 66% percentile of all possible routes. The pigeons were the only travelers to encounter the correction procedure.

Following the conclusion of Experiment 2, the pigeons encountered a 10-day baseline period during which the route-based contingency was not imposed and the routes that the pigeons and the other statistical travelers selected were measured. The baseline performance provided a standard of performance while reexposing the pigeons to problems similar to those encountered in Experiment 2. During the second block of 10 days, the performance criterion was imposed, and the routes that the pigeons selected during the course of a trial had to be shorter than 42% of all routes (a rank of 7 of 12) to advance to the next trial. During the third and fourth blocks of 10 days, the birds were required to select a route that was shorter than 50% of all routes (a rank of 6 of 12) and then a route that was shorter than 66% (a rank of 4 of 12) of all possible routes, respectively, to continue to the next trial of the session. As in Experiment 2, the pigeons encountered 120 trials during each daily session.

Measures and analysis. We calculated the length of the routes selected by the pigeons, the Monte Carlo model, and the nearest neighbor model, as in Experiment 2. We always used the pigeons' first route in a trial, regardless of whether or not it met criterion, for calculating the distance of the route used in the analyses. Thus, performance could not be artificially improved by eliminating from the analyses those routes that failed to meet criterion. In Experiment 3, we wanted to compare performance across the various baseline and manipulation periods to see whether the criterion had an effect on performance. However, comparing performance across these periods could be problematic, as the problems that the travelers encountered were not held constant. Still, any variability in performance across blocks of sessions would be expected to be small given the large number of problems that the travelers encountered in each session. An examination of the data from Experiment 2 indicated that the standard deviation of the average solution for problems with four nodes was 0.52 cm.

Even though this level of variability was small, we decided to calculate measures in this final experiment that reflected the difference in the distance traveled between the pigeons and the Monte Carlo model and between the pigeons and the nearest neighbor model. Both the Monte Carlo and nearest neighbor models provided a standard of performance regardless of changes in the mean distance of all solutions for problems in a session. Changes in the distance of the pigeons' routes compared with these standards should indicate relative, rather than absolute, changes in performance. Therefore, we calculated two difference scores: For the first score, we subtracted the mean length of the route selected by the pigeons in each daily session from the mean length of the routes selected by the Monte Carlo model for the same period (P-MC difference score). This difference score should increase if the routes the pigeons select become shorter when the criterion is imposed. Likewise, we also subtracted the mean length of the routes selected by the pigeons in each daily session from the mean length of the routes selected by the nearest neighbor model in each session (P-NN difference score). This difference score might decrease if the performance criterion were effective in reducing the length of the pigeons' routes. Two one-way ANOVAs then were conducted that used criterion as a variable (baseline, 42%, 50%, 66%) and either the P-MC difference score or the P-NN difference score as a measure.

We also wanted to see how the pigeons might alter their behavior to meet criterion. One possibility is that the pigeons' routes would become more like the nearest neighbor model, that is, the pigeons would select the next closest node in se-

quence until the route was completed. We compared the proportion of the pigeons' routes that matched those selected by the nearest neighbor model during the baseline, 42%, 50%, and 66% conditions in Experiment 3. These data were used in a one-way ANOVA that had performance criterion (baseline, 42%, 50%, 66%) as a repeated measure.

Finally, we conducted the cluster analysis using the data from the pigeons as described in Experiment 2. For each problem (trial), we ranked each leg in a problem from shortest to longest. Because only problems with four nodes were used in Experiment 3, there were six possible legs for any given problem. We then recorded the rank of the leg that the pigeons selected as the first leg for each trial in a session, as described in Experiment 2. These data were used in the cluster analysis as described in Experiment 2.

The results from Experiment 2 indicated that pigeons tended to select the shortest leg of a route as the first leg of their trip for problems with four nodes. It might be the case that the pigeons' tendency to use the shortest leg as the first leg of a route had a strong positive relationship with any tendency to use a nearest neighbor route. That is, pigeons may be more likely to use a nearest neighbor route when first taking a short leg than when first taking a relatively long leg. Therefore, in Experiment 3, we also recorded the number of trials for which the pigeons used the nearest neighbor route (as described in Experiment 2); for those trials, we also recorded the rank of the initial leg of the trip. We then calculated the proportion of occasions that the pigeons used a nearest neighbor route as a function of leg ranking (1 to 6). Thus, the data allowed us to examine any tendency the pigeons might have had for using a nearest neighbor route when starting with initial legs of various lengths. We conducted a repeated measures ANOVA with performance criterion (baseline, 42%, 50%, 66%) and leg rank (1, 2, 3, 4, 5, 6) as variables and the proportion of nearest neighbor routes using a given leg ranking as the first leg of the route as a dependent measure.

Results

The mean difference between the routes selected by the pigeons and those by the Monte Carlo model during baseline (see Figure 8, top panel) was 2.22 cm (*SEM* = 0.41). The difference in route length between these travelers was comparable to that observed in Experiment 2 for problems with four nodes (*M* = 2.74 cm, *SEM* = 0.51, data not shown). The P-MC difference score for the 42% criterion condition was similar to that observed during baseline (*M* = 2.26 cm, *SEM* = 0.60). The difference in performance between the pigeons and the Monte Carlo model increased (3.77 cm, *SEM* = 0.84) when the criterion was set at 50%; it was more than double that observed during baseline (4.83 cm, *SEM* = 0.92) when the pigeons were required to make a trip that was shorter than 66% of all possible routes.

The ANOVA using the P-MC difference score as a dependent measure revealed a main effect of criterion, $F(3, 9) = 10.71$. Subsequent pairwise comparisons indicated that the P-MC difference scores were comparable for the baseline and 42% conditions ($p > .05$). The difference scores for the 50% and 66% conditions were significantly larger than those observed for either the baseline or the 42% condition (all ps < .05). The mean difference scores for the 50% and 66% conditions did not differ from each other ($p > .05$).

The difference in the distance of the routes selected by the pigeons and Monte Carlo model rose as the performance criterion increased and, correspondingly, the distance of the routes selected by the pigeons and the nearest neighbor model fell. The P-NN difference score was –4.53 cm (*SEM* = 0.60) during baseline (see Figure 8, top panel), which was also comparable to that observed in Experiment 2 for all problems with four nodes (–4.11 cm, *SEM* = 0.38). This difference score decreased somewhat as the performance criterion was increased from 42% (–3.94, *SEM* = 0.70) to 50% (–3.33, *SEM* = 0.54), and eventually to 66% (–2.65, *SEM* = 0.63).

An ANOVA using the P-NN difference score as a dependent measure also revealed a main effect of criterion, $F(3, 9) = 11.31$. Subsequent pairwise comparisons indicated that the difference scores were comparable for the baseline and 42% conditions ($p > .05$). The difference scores were smaller when the criterion was set at 50% and 66% compared with when the criterion was set at 42% (ps < .05); the difference scores for the 50% and 66% conditions did not differ from one another ($p > .05$). Levene's tests again failed to indicate a significant difference in error variances for any of the comparisons reported above (all ps > .05).

An average of 32% of the pigeons' routes during testing with four nodes in Experiment 1 were identical to those of the nearest neighbor model; an average of 27% of the routes corresponded with the nearest neighbor model during the baseline condition of Experiment 3. Notably, the percentage of routes that corresponded with the nearest neighbor model increased as the performance criterion became more stringent in Experiment 3. An average of 30% of the routes were identical to those made by the nearest neighbor model for the 42% criterion, but this increased to 38% and 49%, respectively, for the 50% and 66% criterion conditions. ANOVA results indicated a reliable main effect of condition, $F(4, 12) = 20.43$, $p < .05$. Subsequent comparisons indicated that the proportion of routes that matched the nearest neighbor model in Experiment 1 did not differ significantly from that observed during the baseline condition in Experiment 3. The proportion of routes that overlapped those selected by the nearest neighbor model increased significantly during the 50% and 66% conditions compared with baseline (all ps < .05).

The improvement in trip efficiency by the pigeons was also observed in the way the pigeons solved the problems. The proportion of trials that the pigeons selected one of the two shortest legs of a problem as the first leg of a trip increased and one of the two longest legs decreased as the criterion for performance was increased (see Figure 8, bottom panel). ANOVA results indicated a reliable interaction between criterion and leg ranking, $F(15, 45) = 6.78$. The effect of leg was also significant, $F(5, 15) = 22.87$, but the overall effect of criterion was not, $F(3, 15) = 0.51$. Six subsequent follow-up one-way ANOVAs were conducted, each of which examined the effect of criterion (baseline, 42%, 50%, 66%) for the selection of each of the six legs of a problem. The ANOVAs that examined the effect of criterion for legs with a ranking of 1, $F(3, 9) = 21.14$; 2, $F(3, 9) = 7.75$; 5, $F(3, 9) = 4.31$; and 6, $F(3, 9) = 3.80$, indicated a reliable main effect of criterion, but not for legs with a ranking of either 3, $F(3, 9) = 0.25$, or 4, $F(3, 9) = 0.04$. Follow-up comparisons revealed that, when the criterion was set to 50% and 66%, the pigeons were more likely to select the legs with the first and second highest ranking as the first leg of a trip compared with the baseline condition (ps < .05) and less likely to select

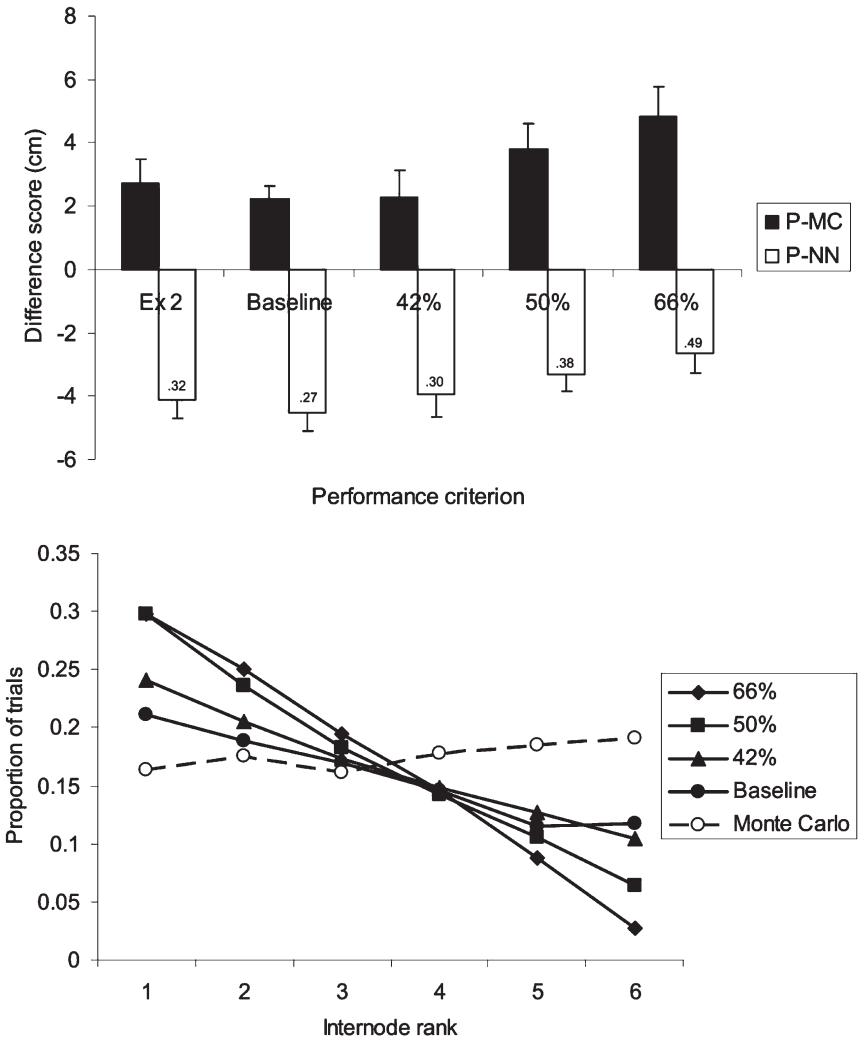

Figure 8. Top: The difference in the length of the routes selected by pigeons and the Monte Carlo model (P-MC; filled bars) and by pigeons and the nearest neighbor model (P-NN; unfilled bars) during the different criterion conditions of Experiment 3. The proportion of trips selected by the pigeons that were identical to those taken by the nearest neighbor model is indicated in the unfilled bar. Bottom: The proportion of trials that each possible leg of a problem was selected as the first leg of a route by pigeons for problems with four nodes for the different criterion conditions (baseline, 42%, 50%, 66%) and by the Monte Carlo model. The possible legs of a problem are rank ordered on the x-axis from shortest (1) to longest (6). Vertical lines depict standard errors of the means.

legs with a ranking of 5 or 6 compared with the baseline condition (ps < .05).

Notably, when pigeons selected a route that was consistent with the nearest neighbor route, they tended to select a shorter, rather than a longer, leg as the first leg of their route (see Figure 9). None of the pigeons' solutions that were consistent with a nearest neighbor route started with a leg that had a rank of 5 or 6 (the longest two legs of a problem) during Experiment 3. When the criterion for performance was increased to 66%, the proportion of nearest neighbor routes that included a leg with a ranking of 1, 2, 3, or 4 as the first leg of the route increased compared with that observed during baseline. Consistent with these trends, ANOVA results revealed a significant interaction between criterion and leg ranking, $F(15, 45) = 5.63$. Six subsequent follow-up one-way ANOVAs were conducted, each of which examined the effect of criterion (baseline, 42%, 50%, 66%) for the selection of each of the six legs of a problem. These ANOVAs again used the proportion of nearest neighbor routes using each of the six leg rankings as the first leg of the route as a dependent measure. There was a significant effect of criterion when legs with a rank of 1, $F(3, 9) = 6.17$; 2, $F(3, 9) = 8.60$; 3, $F(3, 9) = 7.24$; and 4, $F(3, 9) = 13.49$, but not 5, $F(3, 9) = 0.00$, or 6, $F(3, 9) = 0.00$, were used as the first leg of a nearest neighbor route. Least significant difference comparisons indicated that the proportion of routes using a nearest neighbor route was greater when the first leg had a rank of 1, 2, 3, or 4 during the 66% criterion condition than during the baseline condition (all ps < .05). The effects of leg, $F(5, 15) = 215.44$, and criterion, $F(3, 9) = 11.70$, in the omnibus analysis were also significant.

Discussion

The mean distance of the routes selected by the pigeons during the baseline condition of Experiment 3 was similar to that observed during Experiment 2, given comparable prob-

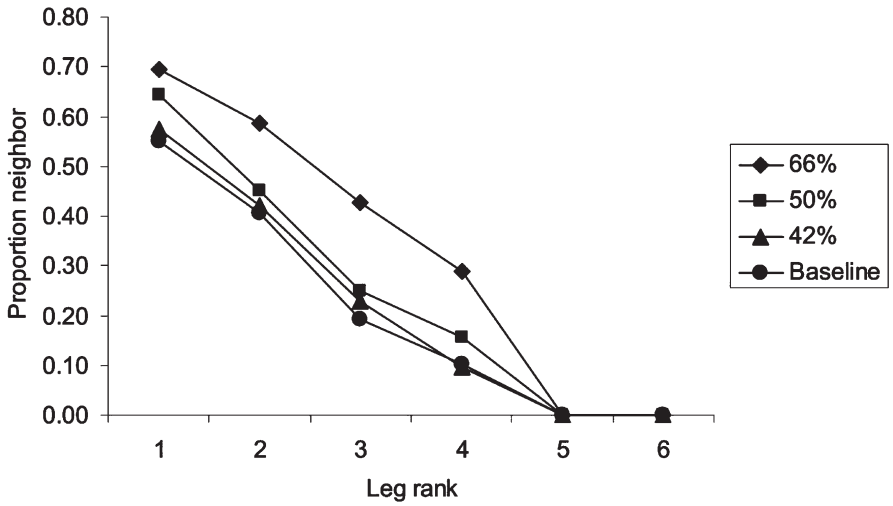

Figure 9. The proportion of routes taken by the pigeons that conformed to the nearest neighbor model during Experiment 3 as a function of the rank (1 to 6) of the first leg used in the nearest neighbor route and performance criterion (baseline, 42%, 50%, 66%).

lems with four nodes. Likewise, the proportion of routes in which the pigeons selected the shortest legs of the problem and avoided the longest legs as the first leg of the route was comparable during baseline in Experiment 3 and Experiment 2. The proportion of trials in which the pigeons' routes matched those selected by the nearest neighbor model was also comparable for problems with four nodes during Experiment 2 and baseline in Experiment 3.

The efficiency of the pigeons' routes improved as the performance criterion increased in Experiment 3. Specifically, the mean distance of the routes selected by the pigeons decreased in comparison to the Monte Carlo model and became more comparable in distance to those routes selected by the nearest neighbor model. The measure of route distance alone does not reveal whether or not the pigeons were using any systematic approaches to be relatively more efficient, only that they became more efficient. One way pigeons may have become more efficient would be by actually using a nearest neighbor route. Indeed, the results indicated that the proportion of the pigeons' routes that matched the routes selected by the nearest neighbor model also increased as the performance criterion increased during Experiment 3.

As in Experiment 2, the pigeons continued to have a strong tendency to include the shortest leg of a problem as the first leg of the trip (cluster analysis), whereas the legs that were longer tended to be avoided. This tendency increased as the criterion for performance was increased. The fact that the birds were selecting the shortest leg as the first leg of a route does not necessarily indicate that this was the mechanism for improved efficiency, only a tendency to select two nodes that were close together. As discussed in the introduction, the pigeons could have taken a long leg first and still arrived at the most efficient route for a given problem (see Figure 1, top row). However, the results from Experiment 3 indicate that not only were the pigeons selecting the shortest leg of a problem as the first leg of their route, they also had a greater tendency to use a nearest neighbor route (a more efficient route) when doing so. Furthermore, as the criterion for performance was increased to 66%, the pigeons' tendency to use the shortest leg as the first leg of a nearest neighbor route increased. The pigeons also started taking more nearest neighbor routes when using legs of intermediate length (Ranks 3 and 4) as the first leg of the route, indicating a possible shift in their behavior as part of the criterion for greater efficiency. The implications of these findings are further discussed below.

General Discussion

Pigeons given one-way TSPs on a video display in Experiment 2 were reliably more efficient than a random model of performance. Furthermore, this result held for problems with three, four, and five nodes. The pigeons' performance in Experiment 2, although reliably better than chance, was significantly worse than the optimal route or the nearest neighbor model, a heuristic for efficiently solving TSPs. We hypothesized that the pigeons' routes may have been less efficient than the optimal and nearest neighbor models in Experiment 2 because the cost of selecting a less efficient route was relatively low. Indeed, the pigeons might have been expected to peck the nodes as quickly as possible without attending at all to the route they were selecting in their haste to obtain food. Using problems with four nodes in Experiment 3, we increased the cost of selecting an inefficient route by requiring the pigeons to select a route that was more efficient than a specified criterion. The criterion dramatically changed the pigeons' performance; the mean distance of the pigeons' routes became progressively shorter than the Monte Carlo model and progressively closer in average distance to the routes selected by the nearest neighbor model as the criterion was made increasingly demanding. Thus, our pigeons were highly sensitive to the costs of selecting an inefficient route and altered their routes accordingly.

In the current study, we were also able to examine any systematic patterns the pigeons may have used to solve the one-way TSPs. One tendency that the pigeons appeared to employ in Experiments 2 and 3, particularly for problems with three and four nodes, was to locate clusters of nodes. The potential legs of a route that connect nodes that are clustered are shorter. Pigeons located and used these shorter legs (to the exclusion of longer legs) as the first leg of a route more often than the Monte Carlo model. The pigeons' routes were consistent with

the routes selected by the nearest neighbor heuristic for about one third of all trials in Experiment 2. The pigeons appeared to search more intensively for clusters of nodes in Experiment 3, where penalties were in force for inefficient travel. The pigeons now included an even larger proportion of the shortest legs in a problem as the first leg of a route as the performance criterion was made more demanding. Likewise, 49% of the pigeons' routes were identical to those used by the nearest neighbor model (66% criterion)—a substantial improvement from Experiment 2, in which 32% of the pigeons' routes were identical to those used by the nearest neighbor model.

The fact that the pigeons selected clusters of nodes initially may imply the use of some type of spatial representation like a cognitive map (for reviews, see Gallistel, 1990; Shettleworth, 1998) that would allow for forward planning of efficient routes. A common test for cognitive mapping has been to examine whether or not an animal can take novel and efficient routes (Bennet, 1996; Shettleworth, 1998). Some researchers instead have sought to determine whether the routes that animals take to visit different configurations of known foraging sites are efficient, suggesting the use of a cognitive map. This work is more consistent with the use of TSPs, as in the current experiment. As noted in the introduction, Menzel (1973) found that chimpanzees did not move at random among a field of 18 baited food sites but tended to take routes that minimized the distance traveled. Likewise, Gallistel and Cramer (1996) reported that vervet monkeys took a route that was most efficient depending on whether or not the monkey was returning to the starting point. In addition, Gallistel and Cramer found that monkeys traveled to large clusters of baited food sites before traveling to smaller clusters of sites that were farther away. Both of these findings suggest the possibility that the vervet monkeys had a representation of the entire set of destinations and planned their routes before starting the trip. More recently, Miyata, Ushitani, Adachi, and Fujita (2006) found evidence that pigeons may preplan routes before leading a target to a goal at the end of a virtual maze.

Were the pigeons in our study using a map-like representation of each TSP problem to plan and select a route? Clearly, the fact that our pigeons were more efficient than the Monte Carlo model suggests they were not selecting nodes at random on most trials. We discovered that pigeons, like other animals, tend to select clusters of nodes first before moving to other nodes in the problem, and that this tendency increased as the criterion for efficiency was made more demanding in Experiment 3. The fact that pigeons selected a relatively large proportion of legs that had the shortest length as the first leg of the route implies that the pigeons scanned much or all of the stimulus display for clusters of nodes before choosing their starting location.

Alternatively, the tendency of pigeons to select clusters of nodes might not indicate the use of a spatial representation or forward planning. The pigeons simply may have been "attracted" to large clusters of nodes on the display. The appearance of clusters of nodes in these problems may have been a powerful stimulus in directing the birds' search, particularly as the criterion for efficiency was made more severe in Experiment 3. The pigeons may have searched more local nodes on the basis of the cues surrounding each previously selected node. Thus, pigeons need not have used a cognitive map to solve the TSP task. Indeed, it is not clear that the human participants in Experiment 1 were using a cognitive map to solve the problems either. A larger proportion of the routes selected by people was identical to those taken by the nearest neighbor model, compared with the performance of pigeons in Experiment 2. The nearest neighbor heuristic, a relatively efficient model for search, could operate using more local stimulus information. Specifically, a pigeon could select an individual node and then continue to select all of the nodes in the immediate visual field before moving to other parts of the screen.

The pigeons also had a strong tendency to start with a relatively short, rather than long, leg of a problem when taking a nearest neighbor route in Experiment 3. In part, this tendency is consistent with the pigeons' overall pattern to start with a short leg of the problem as the first leg of a route regardless of whether or not the pigeons' routes were consistent with the nearest neighbor route. However, the pigeons never took a nearest neighbor route after selecting either the longest (rank = 6) or second longest (rank = 5) leg of a problem during Experiment 3 (see Figure 9, all criterion conditions), even though between 12% and 27% of all of the pigeons' routes first used one of these legs across all criterion conditions (see Figure 8, bottom). Notably, when the criterion was increased to 66%, the pigeons started to include a larger proportion of legs with an intermediate length (Ranks 3 and 4) as the first leg of a nearest neighbor route compared with the baseline condition. Thus, the pigeons' node-selecting behavior changed (other than selecting the shortest leg first as part of a nearest neighbor route) when the conditions for performance changed. Why this shift occurred remains unclear. The pigeons could have used an even larger proportion of the shortest leg across problems as the first leg of the nearest neighbor route. Apparently, the demand for increased efficiency required by the 66% criterion not only resulted in an increase in the proportion of nearest neighbor routes but perhaps some exploration in how the nearest neighbor route was used.

It could be proposed that, although the pigeons selected significantly shorter routes than those chosen by the Monte Carlo model in the current experiments, the actual magnitude of the disparities was relatively small. This proposal might be particularly true for performance in Experiment 2. In part, the size of the differences in route length was limited by the size of the computer screen and the parameters set by the program to construct the stimulus displays. Although the observed differences in path length between the pigeons and the Monte Carlo model may have been relatively small in some cases, such small differences can add up quickly over time. Even small disparities in the selected routes may have important consequences for survival in the natural environment. Animals that use less optimal routes need to expend more energy during the course of the trip, and they may have more exposure to predators.

One difference between the current study and other studies that have used analogues of the TSP is that we presented the pigeons with a large number of diverse problems. The routes that the pigeons selected were relatively efficient across a wide range of problems with different levels of apparent difficulty. As well, and in contrast to other studies, our TSPs were presented on a vertically aligned computer monitor. Although the pigeons were not flying or walking through three-dimensional space to the various locations or nodes in the problem, the same cognitive mechanisms that may be used by pigeons to select a route in the natural environment, for example, foraging for grains, may be applied when selecting among routes to "visit" multiple locations on a computer screen.

To conclude, in the current study, we have discovered that pigeons and people can solve simple one-way TSPs presented on a computer screen. The solutions selected by pigeons were efficient compared with those of a Monte Carlo model of performance but less efficient than the solutions of people. Pigeons exhibited large improvements in efficiency when the cost of making an inefficient route was increased. Thus, analogues of the TSP can be successfully implemented in operant conditioning environments. Future research using the TSP (or analogues of it) would appear to be useful to further explore spatial cognition in human and nonhuman animals.

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